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A MORPHOLOGICAL STUDY ON THE MALE GENITALIA OF *PARACRYPTOCERUS (P.) PUSILLUS.* (HYMENOPTERA: FORMICIDAE)

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(with 13 figures)

During the past three decades the genital apparatus of male Hymenoptera has been the object of extensive research. The importance of this investigation lies not solely in the astonishing increase in the knowledge of morphological and ontogenetic facts. The accumulation of isolated data gave also rise to a highly improved understanding of the homologies of the constituent parts of the genitalia throughout the order of Hymenoptera.

This synthetic and comparative treatment of the subject is mainly the work of two distinguished morphologists: Boulangé (1924) and Snodgrass (1941). However, due to the fact that at the present time a complete knowledge of the genital apparatus is still limited to a comparatively small number of species, it is possible that not all the generalizations, as proposed by these two authors, will invariably hold true. At any rate, they can be regarded as a reasonable and very helpful working hypothesis, which now must be subjected to the test of additional research.

The present contribution consists in an original investigation upon the male copulatory apparatus of a single Neotropical ant, *Paracryptocerus (P.) pusillus* (Klug, 1824). This ant belongs to the tribe Cephalotini, a major subdivision of the subfamily Myrmicinae. It is the purpose of this writer to offer a clear and understandable exposition of the structure and the mechanical set-up of the genitalia of this ant. The terminology, adopted here, is the one proposed by Snodgrass in his paper on the male genitalia of Hymenoptera.

Procedure. — Since only dead and dry specimens of taxonomic collections were available for this study, histological sections and ontogenetic investigations could not be made. But, despite the very inadequate condition of the material, the musculature of the phallic organ turned out to be surprisingly well preserved in all the seven specimens examined. The muscles showed up rather clearly, after the genitalia had been softened in tap water, run through the alcohol series of increasing strength, and cleared in xylene. For the purpose of study under the microscope, the entire material was kept in glycerine. A rudimentary and improvised staining method was given to some of the specimens, which were dipped, for a few seconds, into ordinary red ink. As a consequence, the delicate muscle fibers lost their great transparency, whereas the sclerotized and chitinous parts of the organ did not take on any of the dye and were not obscured. One set of genitalia, taken from a callow male specimen, was preserved *in toto*, because the scarcely pigmented integument was sufficiently transparent to permit the location of the divers muscle strands *in situ*. This specimen was constantly consulted for reference, in each step of the dissection. Two specimens were boiled in a 10% solution of KOH and were used for the study of the skeletal parts.

In the following a description of, and a comment on, the structure of the copulatory apparatus and the pertaining musculature is presented. The accompanying figures have been drawn from the specimens, with the aid of a *camera lucida*.

I. THE EXTERNAL ANATOMY OF THE COPULATORY APPARATUS

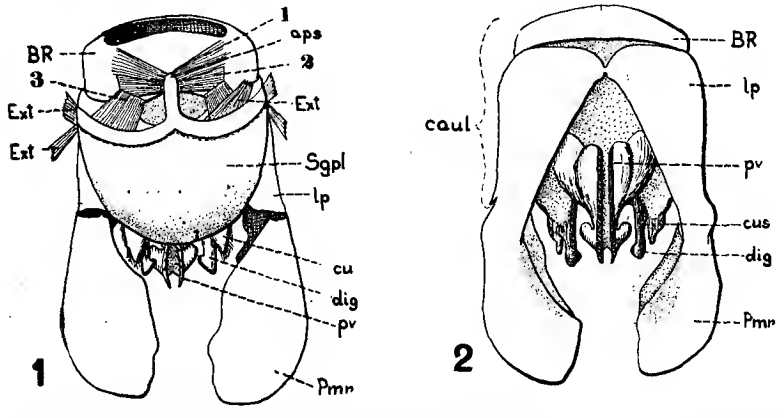
The exoskeletal portions of the genitalia are largely sclerotized. The following parts may be readily distinguished:

1. The entire apparatus rests on the 9th sternite of the abdomen, which, for this reason, termed the *Subgenital Plate* (*Sgpl*). The biconcave anterior border of this sclerite is rather strongly sclerotized and somewhat thickened. It bears in the middle a long and narrow projection, the *Apodeme of the Subgenital Plate* (*aps*), which serves as the point of origin for a part of the extrinsic musculature of the phallus (Figs. 1, 8).

2. The copulatory organ proper, or the phallus, consists of a basal stalk, the phallobase or *caulis* (*caul*), and the apical free lobes. The caulis itself is a compound structure, in which three elements, the single basal ring, and the paired parameral plates and volsellar plates may be recognized. These plates bear the copulatory claspers, that surround the median intromittent organ, the penis or aedoeagus.

a. The *Basal Ring* (*BR*) or *lamina annularis* is a closed sclerotized ring, through which the lumen of the phallus communicates with the general body cavity, and the endophallus with the ejaculatory duct. It should be noted that in the present species no mid-ventral gonocondyles can be found. The extrinsic phallic muscles insert on ventro-lateral ridges, as shown in Fig. 1. Snodgrass points out that the basal ring is a structure peculiar to the order of Hymenoptera (Figs. 1, 2, 3, 4).

b. The pair of *Parameral Plates* (*lp*) or *laminae paramerales* form the basal portion of the large outer genital claspers. They are fused to each other at a single point dorsally, near the base, whereas the ventral longitudinal borders are separate and bent inward along the mid-body line. The basal mid-ventral corner is prolonged into the *Basal Apodeme of the Parameral Plates* (*apr*) which projects foreward under the basal ring. Dorsally the space between each plate is covered by a membranous integument, which is continuous with the dorsal wall of the aedoeagus (Figs. 1, 2, 3, 4, 12, 13).

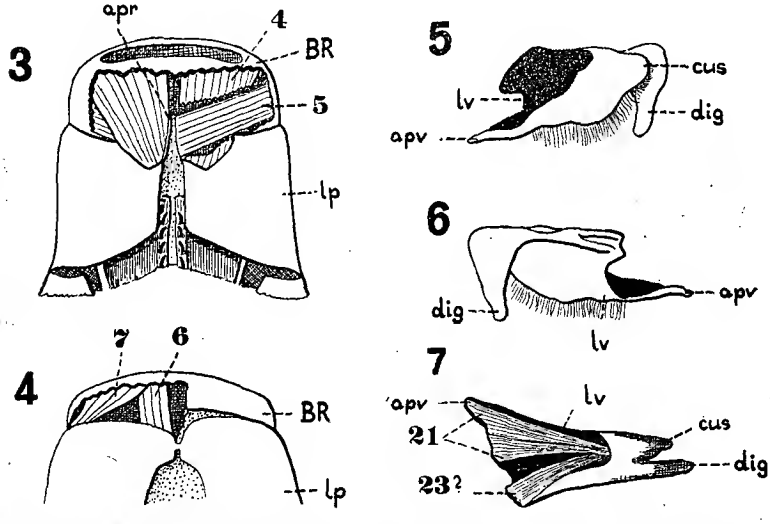


Paracryptocerus pusillus (Klug), — Fig. 1 - Male genitalia with subgenital plate, ventral. Subgenital plate (*Sgpl*), basal ring (*BR*), apodeme of subgenital plate (*aps*), parameral plates (*lp*), parameres (*Pmr*), penial valves (*pv*), digitus (*dig*), cuspis (*cus*), extrinsic musculature of subgenital plate (*Ext*), extrinsic musculature of phallus (*1, 2, 3*); Fig. 2 - Idem, male genitalia, dorsal.

c. The *Parameres* (*Pmr*), often called *stipites* by ant specialists, are the distal processes of the parameral plates, and represent, according to Snodgrass, the sclerotized lateral lobes of the primary phallic lobes of earlier ontogenetic stages. The parameres of the present species are depressed and somewhat spoon-shaped. The inner face is slightly excavated and has the integument

scarcely sclerotized. Since it is this face that is brought into contact with the outer face of the abdomen of the female during copulation, the weak sclerotization may possibly allow a firmer grip by producing the effect of a cupping disc. Dorso-laterally the parameres are continuous and firmly ankylosed with the parameral plates, whereas ventrally they are separated by a transverse slit (Figs. 1, 2, 12, 13).

d. Each of the two *Volsellar Plates* (*lv*) together with their apical lobes, the lateral blunt *Cuspis* (*cus*) and the mesal, hook-shaped *Digitus* (*dig*) form a single continuously sclerotized, inar-



Paracryptocerus pusillus (Klug) — Fig. 3 - Male genitalia, intrinsic musculature (*4, 5*) of caulis, ventral. Basal ring, (*BR*), parameral plate (*lp*), ventro-mesal apodeme of parameral plate (*apr.*); Fig. 4 - Idem, intrinsic musculature of caulis, dorsal (*6, 7*); Fig. 5 - Idem, left volsella, lateral. Volsellar plate (*lv*), apodeme of volsellar plate (*apv*), cuspis (*cus*), digitus (*dig*); Fig. 6 - Idem, left volsella, mesal; Fig. 7 - Idem, right volsella, dorsal. Intrinsic musculature of volsella (*21, 23?*).

ticulate structure, termed the *Volsellae*. They constitute the internal ventral pair of copulatory pincers. The outer proximal end of the volsellar plates is prolonged into the *Apodeme of the Volsellar Plate* (*apv*) and serves for muscle attachment. The distal lobes, i. e. the digitus and the cuspis, do not apparently possess autonomous motion in this species. It is doubtful whether they can be used effectively as pincers to grasp hold on the conjunctival membrane of the vulva of the female during copulation (Figs. 1, 2, 5, 6, 7, 12, 13).

e. The *Aedoeagus* (*Aed*) or penis is the intromittent organ proper. It consists of the median membranous endophallus and the lateral sclerotized *penis valves* (*pv*) of peculiar shape. The aedoeagus lies between the genital claspers and is only loosely connected with the parameral plates by means of muscles. The penis valves are bound to each other by means of the median membranous stripe, which also contains the endophallus. The proximal end of each penial valve bears a long, rod-like, *Basal Apodeme of the Aedoeagus* (*apa*) that points foreward and slightly upward, and laterally the penis valves possess another short, tubercular apodeme, the *"Ergot"* of Boulangé (*e*). Both projections serve as points of insertion for the extrinsic aedoeagal musculature. The ventral border of each penis valve bears a row of small spines, recurved cephalad, and their function probably consists in anchoring the aedoeagus with in the copulatory pouch of the female (Figs. 1, 2, 9, 10, 11, 12, 13).

II. THE MUSCULATURE OF THE COPULATORY APPARATUS

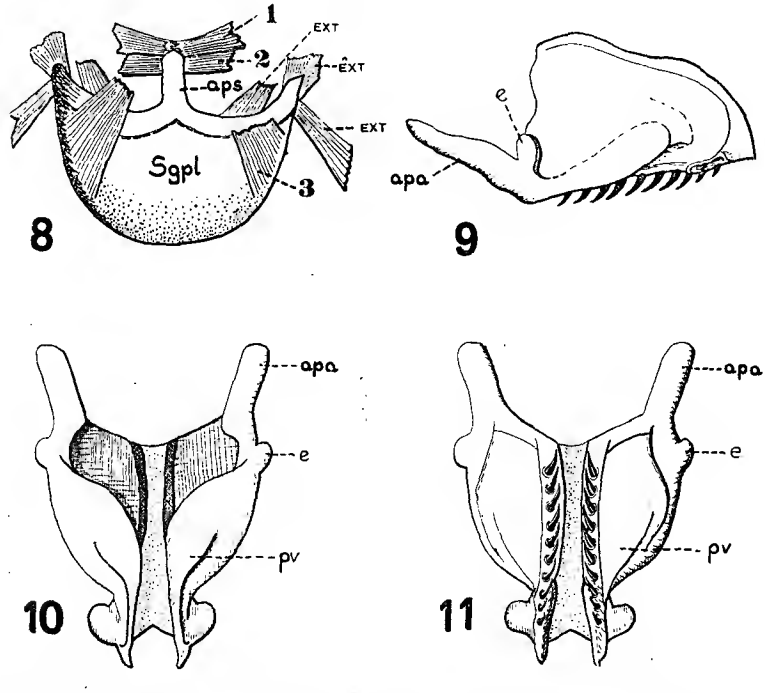
The general patterns of the phallic musculature of Hymenoptera have been outlined in the studies of Boulangé and Snodgrass. It is interesting to notice that the genital muscles of the present species conform themselves rather closely to this basic scheme, with the exception of a few minor deviations to be pointed out below. In order to facilitate the comparison the muscles will be designated with the numbers of Snodgrass, whenever the homology is evident. Incidentally, it should be noted that the homology may be both anatomical and functional, and these two aspects do not always coincide. However, origin and insertion of any given muscle seem to offer the best criterion for the establishment of true homologies.

1. MUSCLES OF THE SUBGENITAL PLATE

The subgenital plate (*Sgpl*) bears two sets of muscles. The first group, consisting of three pairs (*Ext*), attach this sternite to the preceding sternite and tergites. They belong to the general musculature of the abdomen, a consideration of which has been excluded from the present investigation. The second set of muscles forms the extrinsic phallic musculature that links the phallus to the subgenital plate and also controls the protraction and retraction of the copulatory apparatus. Muscles *1* and *2*, both originating from the basal apodeme of the subgenital plate and inserting ventro-laterally on the basal ring, are the retractors. The origin of muscle *3*, the protractor of the phallus, is laterally on the subgenital plate. It inserts on the ventro-lateral ridge of the basal ring (Figs. 1, 8).

2. INTRINSIC MUSCULATURE OF THE CAULIS

Four pairs of muscles, two dorsally and two ventrally, extend between the basal ring and the parameral plates (*lp*). The first pair, or muscle *4* (Figs. 3, 12), arises mid-ventrally on the basal ring and inserts ventrally on the bases of the parameral plates. The second pair, muscle *5*, originates laterally on the basal ring and in-



Paracryptocerus pusillus (Klug) — Fig. 8 - Subgenital plate (*Sgpl*), dorsal. Apodeme of subgenital plate (*aps*), insertion of extrinsic musculature of subgenital plate (*Ext*), origin of extrinsic musculature of phallus (*1, 2, 3*); Fig. 9 - Aedoeagus, lateral. Basal apodeme of aedoeagus (*apa*), "ergot" (*e*); Fig. 10 - Aedoeagus, dorsal. Penial valves (*pv*); Fig. 11 - Aedoeagus, ventral.

serts mesally on the ventro-mesal apodeme of the parameral plate (*apr*) (Figs. 3, 12). This muscle crosses over the preceding muscle. The two dorsal pairs, muscle *6* and *7* (Fig. 4), likewise arise on the basal ring. Muscle *6* is longitudinal, whereas muscle *7* is oblique, inserting laterally on the base of the parameral plates. The function of this group of muscles (*4-7*) is far from being understood. A side from strenghtening the articulate connection between the basal ring and the parameral plates, they may, perhaps,

also be concerned indirectly with the motion of the parameres. Since the latter are more or less firmly ankylosed and continuous with the parameral plates, the alternate action of the muscles *4-7* on the parameral plates could possibly result in a partial adductor, resp. abductor effect on the parameres. At any rate, the present insect lacks the specific parameral muscles, which are found in some of the lower Hymenoptera.

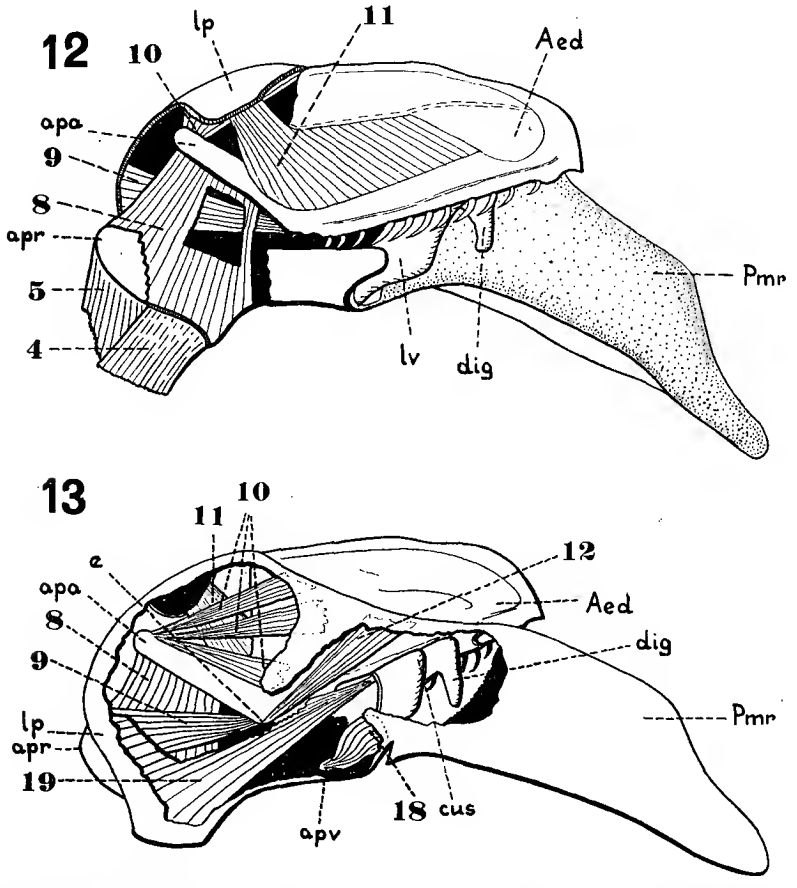
3. THE MUSCULATURE OF THE AEDOEAGUS

Paracryptocerus pusillus possesses the usual five pairs of aedoeagal muscles. Two pairs originate on the proximal ends of the parameral plates, one of which, muscle *8,* going to the apical half of the basal apodeme of the penis valves (*apa*), the other, muscle *9,* to the short lateral apodeme "ergot" of the penis valves (*e*) (Figs. 12, 13). Both muscles are retractors of the aedoeagus. The origin of muscle *10* is from several loosely connected strands, spread out along the dorso-mesal border of the apical half of the parameral plates. These strands extend foreward and fuse to a narrow, tendon-shaped, band, that inserts on the tip of the basal apodeme of the penis valve (*apa*). It functions as a protractor of the aedoeagus. The same function is shared by muscle *12,* which originates somewhat behind the preceding muscle, dorso-laterally on the parameral plate, and inserts on the small lateral apodeme of the penis valve (*e*) (Fig. 13). The last pair of aedoeagal muscles, number *11,* arises dorsally from near the point of contact of both parameral plates. Its insertion is mesally on the proximal portion of the basal apodeme of the penis valves (*apa*) and along the inside of the penis valve. This muscle seems to contain elements of the muscle *14,* a transverse muscle which unites the penis valves and is found sporadically in divers Hymenoptera. At any rate the posterior fibers of *11* do not originate from the parameral plate but rather appear to be attached to the median membranous wall, which extends itself between the penis valves (Fig. 12. The function of muscle *11* partly coincides with the retractor muscles. But, on the other hand, it is also antagonistic to muscle *8* by being capable of raising the basal end of the aedoeagus.

4. THE MUSCULATURE OF THE VOLSELLAE

In more primitive Hymenoptera, which possess a highly complicated volsellar apparatus, the extrinsic and intrinsic muscles of the volsellae are numerous and of an intricate arrangement. In the present species, the pincer-like function of this structure is at most rudimentary. Moreover, the volsellar plates are ankylosed with the parameral plates. This functional reduction is accompanied by a considerable reduction of the musculature. There are

two well developed extrinsic muscles of the volsellae, muscle *18* and *19* (Fig. 13). The former arises from the postero-lateral border of the parameral plate (*lp*) and inserts on the basal apo-



Paracryptocerus pusillus (Klug) — Fig. 12 - Phallus, mid-sagital. Parameral plate (*lp*), paramere (*Pmr*), ventro-mesal apodeme of paramere (*apr*) volsellar plate (*lv*), digitus (*dig*), aedoeagus (*Aed*), basal apodeme of aedoeagus (*apa*), intrinsic musculature of caulis (*4, 5*), extrinsic musculature of aedoeagus (*8, 9, 10, 11*) ; Fig. 13 - Idem, phallus, lateral view, outer wall of parameral plates (*lp*) partly removed. Basal apodeme of volsella (*apv*), cuspis (*cus*), "ergot" (*e*), extrinsic muscles of volsella (*18, 19*), extrinsic muscles of aedoeagus, protractors (*10, 12*), retractors (*8, 9, 11*).

deme of the volsellar plate (*apv*). Obviously, this is an abductor of the volsellae. However, it lacks an antagonistic adductor muscle, that draws is back again towards the parameres. This func-

tion is fulfilled by the elasticity of the volsellar plate. Consequently, as soon as the tension exerted by muscle *18* ceases its pull, the volsellae straighten out immediately to their original position. The second extrinsic muscle, *19*, originates laterally on the base of the parameral plate and inserts dorsally on the volsellae between the digitus and the cuspis. The function of this muscle is not very clear, but may coincide with that of the intrinsic muscle *21*, which arises from the base of the volsellar plate and inserts likewise on the inside of the cleft between the apical lobes of the volsellae. Perhaps the pull exerted by these two muscles upon the integument of the fold between the terminal volsellar lobes, may indeed bring the digitus closer to the cuspis, so that a pincer effect is accomplished. Muscle *23?*, the homology of which is very doubtful, seems to have a similar effect. It arises from the base of the volsellae, mesad of muscle *21* (Fig. 7).

CONCLUSIONS

From the preceding account which contains the examination of the structure of the copulatory apparatus and its musculature it becomes apparent that the copulatory action of the male involves several steps of coordinated movements:

1. After seizing the female, the tip of the abdomen is curved downward and slightly foreward. The structural elements responsible for this movement are the general abdominal muscles which have not been considered here.

2. The entire phallus is then exserted, the parameres lying laterally on the outside of the abdomen of the female, the aedoeagus facing the copulatory pouch. This is accomplished by the strong protractor muscle *3*. Muscles *4-7*, as said before, may possibly be concerned with the clasping movement of the parameres. Furthermore, there is likewise a possibility that the coordinated movements of muscles *18*, *19* and *21* may draw the digitus against the cuspis in a pincer-like fashion to grasp the conjuctiva of the copulatory pouch (Figs. 1, 7, 8, 12, 13).

3. The last step consists in the exsertion of the aedoeagus by means of muscles *10* and *12*. When this is accomplished insemination may take place (Fig. 13).

The reverse movement is executed under the direction of the antagonistic musculature, resp. by means of the elasticity of the structures involved, as it is the case of the volsellae and partly also of the parameres:

1. Retraction of the aedoeagus, accomplished by muscles *8*, *9*, *11* (Figs. 12, 13).

2. Retraction of the entire phallus, due to the action of muscles *1*, *2* (Fig. 1).

3. Straightening of the tip of the abdomen, executed by the general abdominal musculature.

REFERENCES

BOULANGÉ, H. — 1924 - Recherches sur l'appareil copulateur des Hymenoptères et spécialement des Chalastrogastres. Mém. et Trav. Fac. Cathol. Lille, fasc. 28, 444 pgs. 141 text figs., 3 pls.

SNODGRAS, R. E. — 1941 - The male genitalia of Hymenoptera. Smithson. Misc. Coll., vol. 99, n. 14, 86 pgs., 33 pls.